Aquatic Conservation:
Marine and Freshwater Ecosystems

Signal crayfish (Pacifastacus leniusculus) predation upon Atlantic salmon (Salmo salar) eggs

Journal:	*Aquatic Conservation: Marine and Freshwater Ecosystems*
Manuscript ID:	AQC-13-0244.R1
Wiley - Manuscript type:	Short Communication
Date Submitted by the Author:	01-Apr-2014
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Broad habitat type (mandatory) select 1-2:	river < Broad habitat type, stream < Broad habitat type
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Broad taxonomic group or category (mandatory, if relevant to paper) select 1-2:	fish < Broad taxonomic group or category, invertebrates < Broad taxonomic group or category
Impact category (mandatory, if relevant to paper) select 1-2:	alien species < Impact category

SHORT COMMUNICATION

Signal crayfish (*Pacifastacus leniusculus*) predation upon Atlantic salmon (*Salmo salar*) eggs

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ABSTRACT

1. The signal crayfish (*Pacifastacus leniusculus*) is a large, polytrophic crustacean which has invaded waterways across much of Europe. Crayfish predate the eggs of several fish species and egg predation, especially by invasive crayfish, is cited as a likely cause of population decline and a serious concern for the conservation of some fish species including at least one salmonid.
2. Numerically, crayfish populations may be dominated by small individuals, but most studies have investigated egg predation by large crayfish. Evidence for crayfish accessing buried fish eggs is equivocal.
3. The ability of signal crayfish of a range of age groups (and hence, sizes) to predate unburied and buried Atlantic salmon (*Salmo salar*) eggs was investigated in laboratory experiments.
4. Only Age 2+ and older crayfish (24-43 mm carapace length [CL]) significantly reduced egg survival in unburied egg experiments, although some evidence of egg predation was observed with Age 1+ crayfish (16-22 mm CL). Age 0+ crayfish (8-14 mm CL) did not predate salmon eggs. No evidence of substantial excavations or predation upon buried eggs by crayfish of any size class was observed. Binomial logistic regression of egg survival against crayfish CL indicated that mean egg recovery fell below control levels when CL exceeded 16.3 mm.
5. These results suggest that large signal crayfish are likely to pose the greatest threat to salmonid eggs, but that crayfish larger than 16.3 mm CL have the potential to predate eggs.
6. Further research is needed before manual removal or harvesting of signal crayfish are used as conservation measures for Atlantic salmon spawning areas in which signal crayfish occur. Restoration of high-quality salmonid spawning habitat might, however, help to prevent signal crayfish predation of salmonid eggs in addition to broader benefits for salmonid conservation.

KEY WORDS: signal crayfish; salmon; trout; egg predation; invasive species

INTRODUCTION

Over the past thirty years the Atlantic salmon (*Salmo salar* L.) has declined throughout its range and, in some rivers, populations have been lost (ICES, 2011). This decline has occurred despite conservation measures designed to reduce fishing mortality. Populations at the southern edge of their distribution have suffered the greatest decline (Parrish *et al.*, 1998; Jonsson and Jonsson, 2009). These regions often contain the highest human population density with greater associated anthropogenic impacts on the freshwater environment (Parrish *et al.*, 1998). In light of this, additional conservation measures are needed to protect the juvenile freshwater life history stages of Atlantic salmon in such vulnerable populations. To be effective, this approach requires the assessment of previously under-researched areas to ensure management options are evaluated and prioritised appropriately (Russell *et al.*, 2012).

Globally at least one salmonid species, the lake trout (*Salvelinus namaycush* (Walbaum)), is threatened by egg predation from (especially invasive) crayfish (Jonas *et al.*, 2005; Ellrott *et al.*, 2007; Fitzsimons *et al.*, 2007). In Europe the non-native signal crayfish (*Pacifastacus leniusculus*

(Dana)) has invaded many catchments occupied by Atlantic salmon and/or brown trout (*S. trutta* L.). The signal crayfish invasion and resultant loss of native white-clawed crayfish (*Austropotamobius pallipes* (Lereboullet)) populations in Britain are well documented (Holdich and Reeve, 1991; Freeman *et al.*, 2010). Unlike lake trout, brown trout and Atlantic salmon bury their eggs, potentially reducing their vulnerability to crayfish predation. Although crayfish may predate fish eggs (Savino and Miller, 1991; Mueller *et al.*, 2006; Setzer *et al.*, 2011), most of the literature concerns large, adult crayfish in contact with fish eggs on the surface of the substrate.

Crayfish are ectothermic and, thus, generally less active when water temperatures are lower (Bubb *et al.*, 2002). Signal crayfish are known to excavate buried boxes containing potential food items at temperatures between 2.4 and 9.6 °C (Gladman *et al.*, 2012) and some wild signal crayfish have been recorded making local movements at temperatures as low as 1.8 °C (Bubb *et al.*, 2002). This makes it likely that signal crayfish continue to feed actively, presumably using olfactory cues which would persist well in cold water, at temperatures typical of those found in many salmon and trout spawning streams during the period when eggs are buried. Previous experiments involving signal crayfish and buried salmonid eggs have not demonstrated crayfish predation upon these eggs (Edmonds *et al.*, 2011; Gladman *et al.*, 2012). These experiments reached differing conclusions about the ability of signal crayfish to detect and dig for eggs, with Gladman *et al.* (2012) suggesting minimal digging activity in the presence of eggs while Edmonds *et al.* (2011) suggested substantial digging in such circumstances. Additionally, signal and probably other crayfish populations, may be dominated numerically by younger, smaller crayfish (Guan and Wiles, 1996), and these individuals may have better access to buried eggs because they could potentially move through interstitial spaces rather than having to dig to access eggs. In northern English salmonid streams, signal crayfish with a carapace length (CL) of 8-22 mm (representing Age 0+ and 1+ group crayfish) have been captured, using large Surber samplers in late autumn and winter, from within coarse gravel sediment of types used for spawning by salmonids (M.C. Lucas, unpublished data). These crayfish, although not visible at the sediment surface, are present at densities of up to 20 per square metre and have been retrieved up to 150 mm below the sediment surface (M.C. Lucas, unpublished data); within the range of depths at which Atlantic salmon and brown trout eggs are typically buried (Armstrong *et al.*, 2003). The aims of this study were, therefore, to investigate the effects of signal crayfish size and egg burial upon crayfish predation of salmonid eggs.

MATERIALS AND METHODS

Crayfish collection, holding and acclimation

Signal crayfish were taken, under licence, from Wilden Beck, NE England (54°34'56 N; 2°00'16 W), a small tributary of the River Tees, in autumn 2011. The Tees has breeding populations of both Atlantic salmon and brown trout confirmed by the authors during electric fishing for unrelated research (J. Findlay and M.C. Lucas, unpublished data). Signal crayfish were held, under licence, in a secure room of the Durham University Life Sciences Support Unit. The crayfish used were of both sexes, although egg-carrying females were not used because of their potentially lower activity and feeding rates (Bubb *et al.*, 2002). Crayfish were held in a temperature-controlled room with an 8L: 16D photoperiod. All tanks were filled with dechlorinated, aerated mains water which

varied between 7.0 and 9.5 °C, thus representing the middle to upper part of the temperature range during salmonid egg deposition and development (Armstrong *et al.*, 2003).

Crayfish were divided into three groups, based upon size-frequency data from Wilden Beck (M.C. Lucas, unpublished data): Age 0+ crayfish with a carapace length (CL) of 8-14 mm; Age 1+ (CL 16-22 mm) and Age 2+ and older (CL 24-43 mm). Age 2+ and older crayfish, with a carapace length (CL) of 24 mm or greater were held individually in 10 L tanks with a fine layer of gravel covering an undergravel filtration plate and a single shelter. Age 1+ crayfish were held in a 200 L stock tank with numerous shelters, a gravel substrate and an external canister filter at a peak density of approximately 45 per m^2. Age 0+ crayfish were held in an 80 L stock tank, with multiple shelters, a gravel substrate and an undergravel filtration system. The crayfish density in this tank peaked at approximately 100 per m^2. A superabundance of food and shelter were provided in stock tanks throughout the study. Crayfish were acclimatised to the temperature and photoperiod conditions for at least three days before experiments commenced. Crayfish were provided with standardised plant and animal food (carrot *ad libitum* and sinking trout pellets biweekly) prior to experiments. Crayfish were last fed trout pellets 48-72 h prior to their use in experiments.

Salmon egg storage

Eyed Atlantic salmon eggs (mean diameter 5.5 mm) were provided by the Environment Agency's Kielder Hatchery and came from wild River Tyne, NE England, stock. Eggs were stored in a single layer in a holding tank with an external activated carbon canister filter and spray bar. Dead eggs were removed daily. Egg survival to hatching for unused eggs was greater than 95%. Experiments were carried out on recently eyed eggs of 250-300 degree days.

General methods

Egg predation trials were carried out in individual acrylic or glass tanks in which unburied or buried salmon eggs were exposed to single crayfish overnight. Each experiment was repeated ten times with crayfish of each size class. The temperature during experiments was 8.4 - 9.5 °C unless otherwise stated. A 5-6 g disc of standard vegetable food (carrot), with which the crayfish were familiar was provided in each tank as an alternative food source to salmon eggs. To reflect the principally nocturnal activity patterns of crayfish, trials lasted from 20 to 20.5 h and encompassed up to 1 h of light followed by 16 h of darkness and then up to a further 4 h of light. In each experiment, infrared CCTV footage was obtained for two replicate tanks of each crayfish age class to provide contextual information on activity and feeding behaviour. However, the position of crayfish above eggs when feeding was potentially occurring, the difficulty of discerning eggs from the gravel background and insufficient resolution, meant that determination of feeding behaviour was not possible. Subsequently, descriptive observations of crayfish feeding on salmon eggs were made from individual 25-30 mm CL crayfish and salmonid eggs in glass tanks, with no substrate, in daylight, viewed from below.

Following the completion of a set of trials, the position of the crayfish and any evidence of digging behaviour was recorded and the crayfish removed and killed humanely. The remaining eggs

from each tank were separated from the substrate by careful sieving and classified as either: healthy (characterised by an intact outer membrane and normal yellowish-pink colour); damaged (characterised by a broken outer membrane, but with most or all of the contents of the egg still present and still of a pinkish yellow colour, with a moving, but damaged e.g. split yolk sac or bleeding embryo); dead but unbroken (characterised by a whitish colour); and dead and broken eggs (which consisted of broken egg membranes or fragments thereof, sometimes with fragments of tissue attached). All eggs recovered from experimental and preliminary trials were in one of the conditions described above. The substrate, tank and shelter were washed thoroughly in dechlorinated water prior to re-use.

Unburied egg trials

The experimental setup consisted of single crayfish in prewashed glass or acrylic tanks of 320 x 210 x 210 mm, with an undergravel filter mechanism and fresh, dechlorinated water. Crayfish were provided with a shelter formed of a drainpipe cut in half longitudinally and placed on the substrate surface. Prewashed substrate of 10 mm (longest axis) gravel 20-30 mm deep was placed in the bottom of each tank. The 10 mm gravel was used for experiments with unburied eggs because it prevented eggs from falling into interstices and, thereby, made it possible to determine whether or not crayfish would eat salmon eggs when they were readily accessible. In this regard these experiments represented a worst case scenario in which eggs were exposed on sub-optimal potential spawning substrate, for instance by wash out or overcutting. Tests in which a drop of dye was released at the sediment surface showed that dye dispersed throughout the water column over about 5 mins, suggesting that potential odour cues would also be distributed similarly. In each treatment (crayfish present) or control (crayfish absent) tank, ten eggs were placed in a group on the surface of the gravel.

In addition to the ten trials with crayfish of each size class, this experiment was repeated a further ten times with age 1+ and age 2+ and older crayfish (the size classes which appeared capable of predating salmon eggs) . Limitations of the temperature control system in the room meant that these experiments occurred at a slightly lower temperature (7.0-7.4 °C) than the previous unburied egg experiments. Median predation rates did not differ significantly between the higher and lower temperature Age 1+ or 2+ groups (see Results) however, so these were combined to produce a larger sample size for modelling.

Buried egg trials

Gravel with a diameter of 20-40 mm, similar to that used by Edmonds *et al.* (2011), and within the size range typically used by wild salmon for spawning was used for buried egg experiments. The direction of air flow to the undergravel filter was reversed, such that air bubbled up through the substrate near the centre of the tank. Buried eggs were placed at a depth of 8 cm, close to (but not in) the rising bubbles to ensure a flow of oxygenated water over the eggs. This was done to ensure that any egg odours from the buried eggs would be carried upwards out of the gravel by the flow of water, thereby potentially providing some spatial information about the location of

the eggs to predators. Tests in which a drop of dye was released in the egg location showed that within 5 mins period dye had emerged from the gravel and began to disperse in the water column.

Statistical analysis

As egg survival data were non-normally distributed non-parametric Kruskal-Wallis and Mann-Whitney U tests were used for the majority of data analysis. An exception to this was the use of binomial logistic regression on the combined data from all unburied egg trials, since by considering each egg as a trial with two possible outcomes the sample size was far larger (n=500) and the data more normally distributed. Chi square tests of association were used on the combined data from all Age 1+ and Age 2+ trials with unburied eggs to test for differences in the numbers of healthy and dead and broken eggs recovered between trials with male and female crayfish. Statistical analysis was performed using IBM SPSS Statistics 19.

RESULTS

Mean egg recovery exceeded 95% in control experiments for both buried and unburied eggs. All eggs were recovered in healthy condition from the majority of control and Age 0+ crayfish tanks, and all eggs were retrieved in a healthy condition from over half of all Age 0+ and Age 1+ crayfish trials; hence mean values, better reflecting the differences between age groups are shown in Table 1. In the unburied egg trials at 8.4-9.5 °C, crayfish age (and hence size) affected the number of both healthy (Kruskal-Wallis test $H = 18.2$, $p < 0.001$) and dead and broken (Kruskal-Wallis test $H = 18.7$, $p < 0.001$) eggs recovered. Subsequent Mann-Whitney U tests (with a Bonferroni correction applied) revealed that the median number of healthy eggs recovered was significantly lower in the Age 2+ and older group than in the control ($U = 12$, $p < 0.005$) or Age 0+ ($U = 10$, $p < 0.005$) groups. The median number of dead and broken eggs recovered was significantly higher in the Age 2+ and older group than in the control ($U = 10$, $p < 0.005$) or Age 0+ ($U = 10$, $p < 0.005$) groups. The minimum CL of crayfish in trials where dead and broken eggs were recovered was 17.6 mm. All the eggs added to trials with Age 0+ crayfish were recovered in healthy condition, hence there was no evidence of any predation upon eggs by crayfish of this age/size class. Video records showed crayfish spending time in areas with exposed eggs, but the camera angle and mouthpart position of crayfish precluded images of egg handling. Subsequent observations of individual 25-30 mm CL crayfish in glass aquaria with showed that crayfish primarily used the second and third pereopods to manipulate eggs to the mouthparts where they were opened, although on occasion eggs were crushed with the chelipeds. Yolk was removed from the eggs, by the small chelae of the anterior pereopods and by the mouthparts, leaving much of the outer membrane intact. No evidence of crayfish digging for eggs was observed in any experiment although some Age 2 + crayfish produced excavations about 10 mm deep in the corners of the tanks in which they were observed to shelter. No evidence for a significant effect of crayfish size/age class on the number of healthy eggs recovered from buried egg trials was observed (Kruskal-Wallis test $H = 2.32$, $p = 0.131$). No damaged eggs were recovered from any experiment.

There were no significant differences in the carapace lengths, the number of healthy eggs recovered, or the number of dead/broken eggs for Age 1+ or Age 2+ and older crayfish between the 8.4-9.5 °C and 7.0-7.4°C trials with unburied eggs. Data from all trials with unburied eggs were, therefore, combined to generate a larger data set to model the relationship between crayfish CL and the number of healthy eggs recovered, using binomial logistic regression (Figure 1). A Wald test of the model showed that the number of healthy eggs recovered was significantly negatively related to crayfish CL (n = 500, β = -0.210, W = 88.0, $p < 0.001$). In this model, the probability of each egg being recovered healthy first fell below control levels when crayfish CL exceeded 16.3 mm (Figure 1).

Across all experiments with unburied eggs and Age 2+ and older crayfish, significantly more healthy eggs and fewer dead and broken eggs were recovered from trials with female crayfish than from those with male crayfish (χ^2 = 25.3, df =3, $p < 0.0001$). No significant evidence was found of any differences in egg recovery rates between Age 1+ male and female crayfish (χ^2 = 0.897, df =3, p = 0.826).

Discussion

This study demonstrated a size effect of signal crayfish on susceptibility of Atlantic salmon eggs to predation, and suggested that unburied eggs are much more vulnerable to crayfish predation than buried ones. The significant difference in the recovery rate between the control and Age 2+ and older experiments provides strong evidence that signal crayfish exceeding 24 mm CL will feed upon exposed salmon eggs in the presence of alternative, familiar food. Dead and broken eggs were only recovered from trials with Age 1+ and older crayfish. Thus, although Age 1 + crayfish did not significantly reduce the number of healthy eggs recovered, the presence of dead and broken eggs in some of the trials involving this age/size class indicates that Age 1+ crayfish are probably capable of predating, and certainly capable of damaging, unburied salmon eggs. The size threshold at which the likelihood of egg recovery dropped below control levels in the model produced by binomial logistic regression also suggests that Age 1+ crayfish (CL > 16.3 mm) might be capable of preying upon salmon eggs. There was no evidence to suggest that crayfish with a CL < 14 mm were capable of predating salmon eggs. As such, although the young of the year, which make up a high proportion of signal crayfish populations especially in the autumn (Guan and Wiles, 1996), are unlikely to be a threat to salmon eggs, it is probable that Age 1+ crayfish and not just the large Age 2+ (and older) individuals could predate salmonid eggs. While in this study, small crayfish did not move through the 20-40 mm substrate, in the wild they can be found within substrate interstices of particles sizes associated with salmon spawning, where access to eggs and alevins is possible (Bubb, 2004; Ream, 2010; M.C Lucas, unpublished data).

The minimum carapace lengths for crayfish predation upon salmonid eggs observed (17.6 mm) and predicted (16.3 mm) define the likely size threshold of impact. Previous investigations report a size effect for rusty crayfish (*Orconectes rusticus* (Girard)), but not virile crayfish (*O. virilis* (Hagen), predation upon bluegill (*Lepomis macrochrus* (Rafinesque)) eggs (Morse *et al.*, 2013). The results of the current investigation indicate that direct foraging by Age 0+ signal crayfish in salmon redds is unlikely, but that even relatively small signal crayfish may be a threat to encountered salmonid eggs, for instance those exposed as a result of the digging activity of later spawning fish or

washed out of redds. Brown trout eggs (4-5 mm diameter) are smaller than those of Atlantic salmon (5-7 mm diameter) (Maitland and Campbell, 1992) and, thus, might be vulnerable to predation from smaller signal crayfish. The reduction in egg survival in the presence of Age 1+ and Age 2+ crayfish is thought to be the result of predation rather than mechanical damage. This is because there was little material left on the insides of the dead and broken eggs, or found elsewhere in the tanks from which dead and broken eggs were recovered. The lack of evidence of digging further reduces the likelihood that eggs were damaged incidentally during the movement or winnowing of sediment. Our observations in glass tanks with no substrate also showed that 25-30 mm CL signal crayfish directly predated eggs.

Age 1+ signal crayfish of both sexes apparently had a similar effect upon egg recovery rates. However, among the larger (Age 2+ and older) signal crayfish, male crayfish had a greater effect upon egg recovery rates than female signal crayfish. This would suggest that male crayfish may pose a greater threat to eggs than female crayfish, although this difference may also relate to the fact that the mean CL for male signal crayfish in this size class (34.0 mm) was larger than that of female crayfish in this size class (28.1 mm). Given the small sample sizes multifactorial testing was not attempted to separate the effects of size and sex upon egg predation rates.

Experimental duration was probably sufficient to observe digging behaviour as another study has demonstrated considerable digging by crayfish within 24 h when in enclosures with pieces of buried herring (*Clupea harengus* L.)(Gladman *et al.*, 2012). That study also observed no substantive digging by crayfish in the presence of salmon eggs. Potentially conflicting results have been observed (Edmonds *et al.*, 2011) with the deepest excavation produced by signal crayfish in an experiment with buried sea trout (*S. trutta*) eggs averaging 97 mm (N. Edmonds *et al*. pers. comm.). Those experiments ran for 64 days, far longer than the longest trials run by Gladman *et al.*, (2012). Nevertheless, Gladman's trials were clearly long enough to allow for digging activity if healthy eggs are readily identifiable, by odour alone, as food. The greater duration of Edmonds *et al.*'s (2011) experiment might have allowed for natural death and decomposition of eggs, or the hatching of the eggs and the metabolism of the resulting embryos, which could then release odour cues more readily recognised by crayfish as indicative of food. Bacterial decomposition of molecules released by potential food items may also be important in producing the appropriate cues to trigger crayfish feeding responses (Hazlett, 1994). If crayfish can detect any chemical cues produced by healthy eggs then either contact with healthy eggs washed out of their redd or exposed by later spawning fish, or attraction to decomposing or hatched eggs might result in this odour being associated with food. This might then cause crayfish to dig out and predate healthy eggs.

Another possible explanation for the difference in results between this study and that of Edmonds *et al.* (2011) is that the signal crayfish used in the latter came from a population which was sympatric with brown trout. The signal crayfish used here came from a tributary of the upper River Tees; Atlantic salmon and brown trout occur throughout much of the Tees' catchment (Williams *et al.*, 2009). However, no salmonids were caught during electric fishing of about 100 m^2 of Wilden Beck for unrelated research (J.D.S. Findlay, unpublished data). There are no obvious barriers to the movement of salmonids from the Tees, up Wilden Beck, to the collection site, and water quality is suitable (J.D.S. Findlay, unpublished data); thus it is likely that salmonids occur in Wilden Beck, but at very low densities. Experiments investigating the attraction of rusty crayfish to walleye (*Sander vitreus* (Mitchill)) egg cues indicated that attraction was a conditioned response produced by

simultaneous exposure to egg and food cues (Weisbord *et al.*, 2012). A similar experiment involving multiple crayfish species demonstrated that contact with food items could also produce a feeding response, after which the odour would be sufficient to produce an attraction response (Hazlett, 1994). However, in virile crayfish this feeding response was only maintained for between 3 and 6 weeks without further experience of the odour (Hazlett, 1994). Therefore, although it is unlikely that the signal crayfish population of Wilden Beck as a whole was naive to salmonids, it is possible that some individuals were functionally naive to salmonid eggs.

The importance of flow to crayfish responses was not investigated in these experiments other than ensuring an upward water movement was generated in buried egg experiments. The presence or absence of flow may be an important determinant of crayfish behaviour and the strength of their responses to odour cues (Pecor and Hazlett, 2006). Future experiments should aim to recreate the physical structure of, and flow patterns found within, redds as accurately as possible.

Further research is also needed to investigate how different-sized crayfish handle fish eggs during predation. Other authors have noted a short handling time for large (37-50 mm CL) virile crayfish feeding upon rainbow trout eggs (Love and Savino, 1993) but simply stated that eggs 'required no handling prior to consumption', implying that eggs were broken and eaten using only the maxillipeds and other mouthparts. Signal crayfish predate pond snails (*Lymnaea stagnalis* L.) by holding the snail with their walking legs and then breaking the aperture with their maxillipeds, in contrast to crabs which break snail shells using their chelae (Nystrom and Perez, 1998). Signal crayfish do, however, use their chelipeds when handling some prey items such as fish (Guan and Wiles, 1997) and did so infrequently in current observations of egg-handling in aquaria with no substrate. Signal crayfish can exclude the native bullhead (*Cottus gobio* L.)from shelters (Bubb *et al.*, 2009) and are potential predators of its eggs although more research is needed into whether such predation occurs and its impacts.

As larger crayfish appear more efficient predators of Atlantic salmon eggs than small ones, the removal of large individuals in spawning areas might reduce the predation pressure to which fish eggs are exposed (Morse *et al.*, 2013). However, the fact that even relatively small signal crayfish may reduce the survival of salmonid eggs is important because most conventional crayfish control methods are ineffective at reducing the numbers of these animals. Hand searching and baited trapping result in catches heavily biased toward larger individuals, potentially allowing for greater feeding activity and faster growth in the remaining, predominantly smaller individuals, which are subject to reduced pressure from cannibalistic predation and competition (Gherardi *et al.*, 2011; Moorhouse and Macdonald, 2011). Trapping, in particular, even when performed with fine mesh traps (5 mm diagonal mesh) appears not to capture crayfish with a CL less than 19 mm (Peay, 2001). Additionally, although smaller crayfish may be individually less damaging, they are generally far more abundant in populations of both signal and white-clawed crayfish than larger animals (Guan and Wiles, 1996). More research is, therefore, necessary before trapping or hand searching could be recommended as a potential salmonid conservation measure. By contrast, given the efficacy of egg burial in preventing signal crayfish predation upon Atlantic salmon eggs, habitat enhancements to increase the area and depth of Atlantic salmon and brown trout spawning gravel in areas where these have been depleted by anthropogenic damage could prove to be a more effective conservation measure. This conclusion does, however, assume that signal crayfish will not dig redds

containing decaying and/or hatched eggs, or eggs buried in more natural flow conditions, and both of these assumptions require testing.

ACKNOWLEDGEMENTS

We are grateful to Richard Bond of the Environment Agency for the supply of salmon eggs. John D. S. Findlay is grateful for funding from the Tees Rivers Trust and Cefas.

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Table 1. The maximum, minimum and mean number of healthy (pink-yellow colour and intact membrane) and mean numbers of dead but unbroken (white colour and intact membrane) and dead and broken (broken membrane with little if any material remaining inside) eggs recovered from tanks subject to each crayfish treatment, *n* = 10 in all cases. No damaged eggs were recovered in any treatment.

Treatment		Maximum healthy	Minimum healthy	Mean healthy	Mean dead but unbroken	Mean dead and broken
Control	Surface 1	10	9	9.8	0	0
	Buried	10	8	9.6	0	0
Age 0+	Surface 1	10	10	10	0	0
	Buried	10	9	9.7	0.1	0
Age 1+	Surface 1	10	7	9.0	0.1	0.7
	Buried	10	9	9.8	0	0
	Surface 2	10	8	9.6	0	0.3
Age 2+ and over	Surface 1	10	4	7.3	0.1	1.1
	Buried	10	8	9.4	0	0
	Surface 2	10	0	6.1	0	1.0

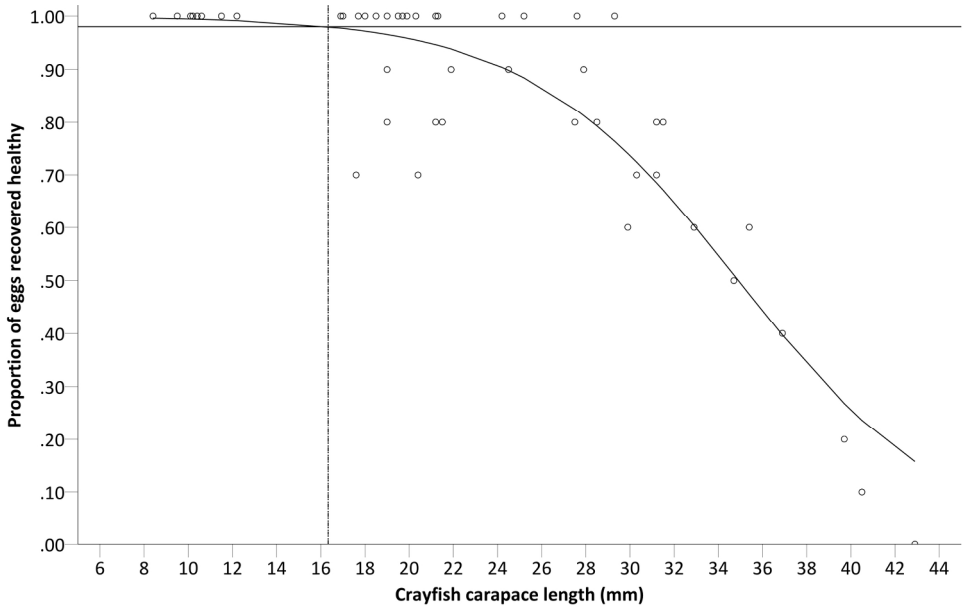

Figure 1: The proportion of exposed salmon eggs being recovered in healthy condition against signal crayfish carapace length (CL). The curved line shows the relationship modelled by binary logistic regression between crayfish CL and the likelihood of each egg being recovered in a healthy condition. The horizontal reference line shows the mean proportion of healthy eggs recovered in control trials (0.98) and the vertical line the crayfish CL at which the likelihood of each egg being recovered in a healthy condition falls below that level (16.3mm).

95x70mm (600 x 600 DPI)